ZOOLOGIA 40: e22044
ISSN 1984-4689 (online)
scielo.br/zool

RESEARCH ARTICLE

Migratory fishes from rivers to reservoirs: seasonal and longitudinal perspectives

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https://zoobank.org/C9916E50-BE1D-4577-83CA-FE11AD53C0FA

ABSTRACT. Migratory fishes have high ecological, social, and commercial value, and are strongly affected by river regulation. This study aimed to understand how migratory fishes use the longitudinal gradient, in an upstream to downstream direction of two free-flowing rivers and two reservoirs in a cascade within the Upper Grande River Basin, Brazil. The numeric abundance, biomass, richness, presence of fingerlings and juveniles, and the macroscopic gonadal maturation stage of migratory fishes were ascertained and evaluated bimonthly for two years. Recruitment in migratory fishes seems to rely completely on the free-flowing rivers upstream and their floodplains. Transition areas do not seem to have a significant role in recruitment. Therefore, we highlight the importance of maintaining the free flow of rivers and the integrity of their floodplains.

KEY WORDS. Recruitment, reservoir cascade, free rivers, freshwater fish.

INTRODUCTION

Migratory fishes are ecologically, socially and commercially important (Harvey and Carolsfeld 2003, Agostinho et al. 2007a, 2016, Pelicice and Agostinho 2008, Pelicice et al. 2018). Most species travel great distances during their life cycle. Their reproductive process, early development and recruitment depend on the natural flow regimen of the rivers they travel in (Gomes and Miranda 2001, Pelicice and Agostinho 2008, Pompeu et al. 2012, Agostinho et al. 2016, Winemiller et al. 2016).

The general reproductive migration pattern of Neotropical freshwater fish includes an upstream displacement in rivers and their tributaries in the beginning of the wet season, followed by spawning. Spawning is triggered by a specific flow events and conditions such as water turbidity and temperature (Harvey and Carolsfeld 2003, Agostinho et al. 2007a, Pelicice and Agostinho 2008, Pompeu et al. 2012, Lopes et al. 2018). After spawning, the eggs develop and hatch as they are passively transported by the river currents to lateral depressions (floodplain lakes), which flood when the water overflows; although floodplains are considered the main nursery areas for fingerlings, they can also develop in the riverbed (Harvey and Carolsfeld 2003, Agostinho et al. 2007a, 2007b, Pelicice and Agostinho 2008, Pelicice et al. 2015, Lopes et al. 2019). The adult parents return to feeding areas where there are more resources and juvenile fishes are eventually recruited (Lucas and Baras 2001, Pompeu et al. 2012, Lopes et al. 2019).

Although the pattern described above has been observed in many river systems, Neotropical migratory fishes may use the habitat differently during reproduction, especially in their early development, depending on the characteristics of the river basin. In rivers without floodplain lakes and similar environments, transient environments between tributaries and the main river channel sometimes provide sufficient conditions and are used as nurseries (Zaniboni-Filho and Schulz 2003, Silva et al. 2020). In the case of rivers that are regulated by dams, the free-flowing stretches upstream of the reservoir determine the maintenance of the diversity of rheophilic fish, since they may allow migratory species to complete their life cycle (Marques et al. 2018, Carvajal-Quintero et al. 2019, Lopes et al. 2019). In these cases, the river-reservoir transition may function as a recruitment area for migratory species. This transitional area provides conditions that are similar to those found in floodplain lagoons, for instance less water turbidity and lentic areas with lateral vegetation, providing refuges and food resources for fingerlings and juveniles (Zaniboni-Filho and Schulz 2003).

Some studies have documented the presence of eggs and larvae in the upper portion of reservoirs (Suzuki et al. 2011, Souza 2013), after which survival and recruitment have not been confirmed. The presence of fingerlings and juveniles in the river-reservoir transition are a sign that migratory fishes can complete their life cycles in the upper areas of reservoirs that have free-flowing stretches upstream. This information is crucial, especially in reservoir cascades, because these free-flowing stretches can intensify the impact on migratory species (Santos et al. 2017, Loures and Pompeu 2018, Santos et al. 2018). Reservoir cascades tend to decrease the numbers of migratory fishes towards downstream reservoirs (Santos et al. 2017), while their richness tends to be higher in reservoirs that present lotic stretches upstream of the impounded area (Loures and Pompeu 2018).

This study aimed to evaluate how migratory fishes use the longitudinal gradient, in an upstream to downstream direction, along two free-flowing rivers and two reservoirs, in a cascade located in the Upper Grande River Basin, state of Minas Gerais, Brazil. We tested three hypotheses: 1) due to their rheophilic behavior and movements along critical habitats, the numbers, biomass, and richness of migratory fishes will decrease from the free-flowing rivers towards the reservoirs; 2) the river-reservoir transition and the floodplain lagoons along the free-flowing stretches of the Aiuruoca and Grande rivers allow the early development of migratory species; and 3) migratory fishes, in mature and post-spawning gonadal maturation stages, will be found predominantly in free-flowing rivers during the wet season.

MATERIAL AND METHODS

Study area

This study was conducted in the Grande River, Upper Paraná River Basin. The Grande River has 12 hydropower dams. In its upper course, stretches of free flowing rivers are still found (Suzuki et al. 2011, Borges and Abjaudi 2016). The longest ones, the Aiuruoca and Grande rivers, flow to the first reservoir, created by the Camargos Hydropower Plant. It started operating in 1960, with a power generation capacity of 45 MW and a reservoir with an accumulated area of 73.35 km². The Itutinga Reservoir, built in 1955, is located immediately downstream of the Camargos Dam and presents an installed capacity of 52 MW and a reservoir area of 1.72 km² (Cachapuz 2006). Both plants coordinate operations (Cachapuz 2006), with a 14-day water residence time (Suzuki et al. 2011). The climate of the study area is classified as semi-humid and mesothermal, presenting annual average temperatures ranging from 18 to 29 °C and annual mean precipitation from 1,450 to 1,600 mm, with four to five dry months (May to September) (Borges and Abjaudi 2016).

The Camargos Reservoir is a storage type and the water levels there can fluctuate up to 14 m, depending on the rainfall volume. The Itutinga Reservoir, which is a run-of-river plant, is more stable in terms of water level fluctuations.

Sampling

We sampled 12 sites, separated by approximately 10 km from each other, distributed throughout the Aiuruoca and Grande rivers and Camargos and Itutinga reservoirs. Also, four marginal lagoons were sampled in Aiuruoca and four in Grande River. In Itutinga, there are no significant tributaries flowing to the reservoir (Fig. 1). Conversely, the Aiuruoca and Grande rivers merge to become the Camargos Reservoir.

We sampled fish every two months between March 2019 and December 2021 in Riv3, Riv4, Trans1, Trans2, Trans3, Cam1, Cam2, Cam3, Itu1 and Itu2, conducting over 12 surveys, six in the dry and six in the wet season. After the first year of sampling, we added two new sites upstream, to maximize the chance of sampling migratory fishes. Therefore, we sampled Riv1 and Riv2 bimonthly with the other sites between September 2020 and December 2021. We captured fish using gill nets with different mesh sizes 3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm, measured by opposite knots, with each gill net measuring 10 m long. The gill nets were set in littoral areas in the afternoon and removed the following morning, totaling 12 hours of exposure. We also used two semicircular hand nets (80 cm in diameter, 1 mm mesh size), 20 minutes per sampling site, and five hauls of beach seines per sampling site (5 m long, 2 m high, and 5 mm mesh size between opposite knots) to collect fingerling and juvenile migratory fishes. At sampling site Riv3, it was not possible to perform beach seine sampling in March due to depths of over 2 m in littoral areas.

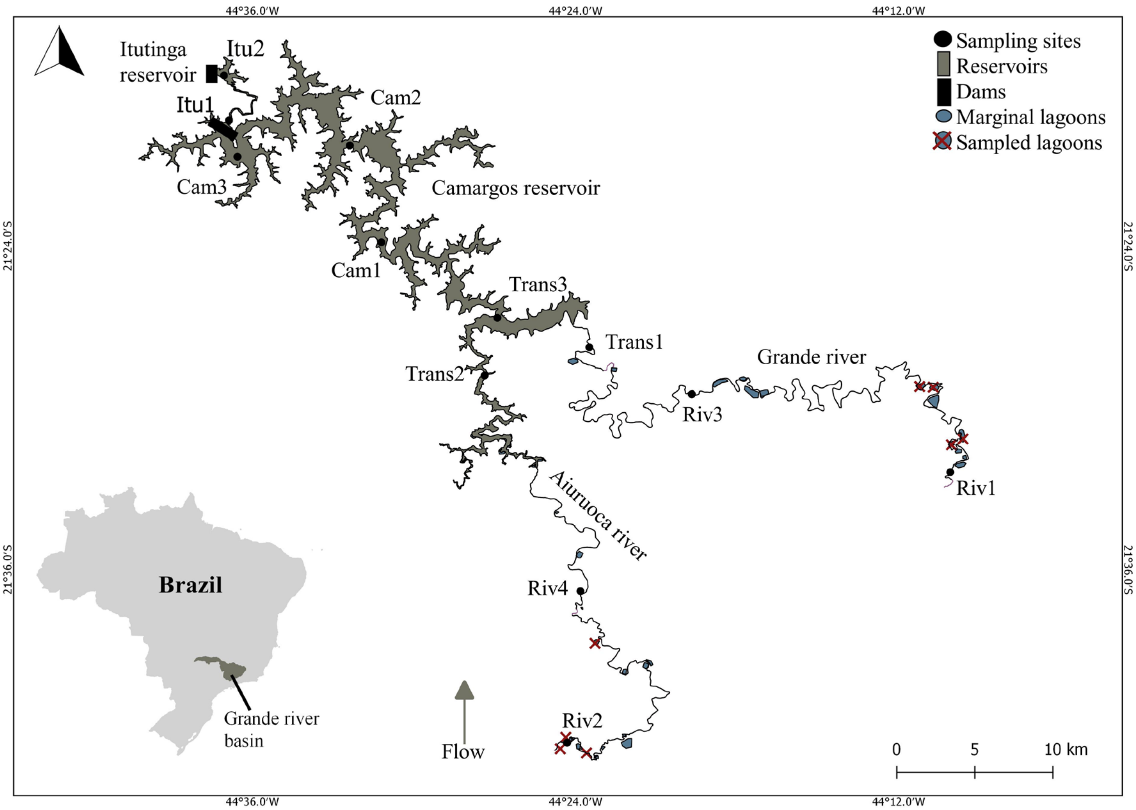

Figure 1. Geographic location and sampling sites in the Grande River Basin, Minas Gerais.Riv: River; Trans: Transition, Cam: Camargos UHE; Itu: Itutinga UHE. More sampling sites details in Table 2.

We sampled within four lagoons in the Grande River and four in the Aiuruoca River in order to determine if these areas are used during the early development and further recruitment of migratory fishes. We employed gill nets (2.4, 3, 4, 5 and 6 cm, measured by opposite knots), semicircular hand nets, and beach seines, with the same standardized sampling effort as in the other sampling sites.

Fishes were anesthetized in Eugenol 50mg/l. We evaluated the gonadal maturation stages based of migratory species based on macroscopic characteristics. Specimens were dissected to determine sex and gonadal stage according to Vazzoler (1996) (Table 1). Instituto Chico Mendes de Conservação da Biodiversidade authorized fish collection (License # 72534) and the Ethics Committee on Animal Use/CEUA of the Universidade Federal de Lavras approved the project (protocol # 112/18).

After gonadal characterization, fishes were fixed in 10% formalin solution and transferred to a solution of 70% alcohol for conservation. In the laboratory, each individual was measured (total and standard body length in mm), weighed (g), classified (Nakatani et al. 2001, Ota et al. 2018, Ribeiro et al. 2019) and their migratory status was confirmed (Agostinho et

Table 1. Classification of gonadal maturation stages of male and female based on macroscopic characteristics (Vazzoler 1996).

Stage	Female	Male
Immature	F1: Thin and transparent ovaries with low vascularity evident, very small in size.	M1: Thin, translucent and reduced testicles.
Initial maturation	F2: Bulky ovaries occupying about 1/3 to 2/3 of the celomatic cavity, oocytes are visible to naked eye.	M2: Bulky testicles with lobed shape, milky white in color.
Mature	F3: Ovaries reach maximum volume, turgid and with numerous oocytes visible to the naked eye.	M3: Testicles are bulky, turgid, whitish. With weak pressure the membrane breaks, releasing sperm.
Post-spawning	F4: Flaccid ovaries with hemorrhagic areas, occupying less than 1/3 of the celomatic cavity.	M4: Flaccid testicles with a hemorrhagic aspect.

al. 2003, 2007a) confirmed. Voucher specimens were deposited in the Ichthyologic Collection of Federal University of Lavras (CI – UFLA 1263, 1264,1271,1261, 1273, 1289, 1268).

Data analysis

In order to understand the general patterns along the longitudinal gradient, data from the sites were grouped in four regions (River, Transition, Camargos and Itutinga) with similar hydrological conditions and characteristics (Table 2). To evaluate the possible differences in numbers, biomass, and richness among groups, we used the Kruskal-Wallis test. Differences among dry and wet seasons were tested for each group using a Wilcox test. We quantified fingerlings and juveniles of migratory species per sampling site using the literature data on fingerlings' maximum sizes and the size of each species at first sexual maturation (Lopes et al. 2000, Nakatani et al. 2001, Esguícero and Arcifa 2010). To assess the second hypothesis and evaluate if the river-reservoir transition areas allow the development of migratory species and to determine how adults use the system, we plotted the number of individuals in each stage (fingerlings, juveniles, and adults) in both seasons. To assess the third hypothesis, gonadal maturation stages were visually compared between regions, in between the wet and dry seasons.

We produced the maps in QGIS (version 2.18.22) with GRASS 7.4.1 and performed the statistical analysis and graphs in RStudio software, v. 1.4.1717 (RStudio Team 2021) using "vegan" (Oksanen et al. 2020) and "ggplot2" (Wickham 2016) packages.

RESULTS

We sampled a total of 898 individuals belonging to seven migratory fish species, corresponding to six genera, four families and two orders (Table 3).

We observed significant differences in numeric abundance (CPUEn: KW = 15.996; $p < 0.05$), richness (KW = 14.583; $p < 0.05$) and biomass (KW = 21.286; $p < 0.05$) among the regions (Fig. 2), with a general tendency for these numbers to decrease along the gradient. However, there were no seasonal differences in numeric abundance, richness and biomass.

Fingerlings, juveniles, and adults of migratory species were registered throughout the entire system. Although we failed to detect a unique pattern for each, we identified some trends. In general, migratory species tend to be found in greater numbers in the stretches of free-flowing rivers and transition zones. Juveniles of six migratory fish species and fingerlings of only one, *Leporinus friderici* (Bloch, 1794),

Table 2. Sampling sites and groups formed considering similar hydrological conditions and characteristics. Marginal lagoons were also represented only to characterize the area.

Sites	Groups	Characteristics	Coordinates
Riv1	River	The lotic section of the Grande River, upstream of the Camargos Reservoir. Marginal lagoons sampled.	-21.539722°, -44.168055°
Riv2	River	The lotic section of the Aiuruoca River, upstream of the Camargos Reservoir. Marginal lagoons sampled.	-21.706944°, -44.405277°
Riv3	River	The lotic section of the Grande River, upstream of the Camargos Reservoir.	-21.491529°, -44.328130°
Riv4	River	The lotic section of the Aiuruoca River, upstream of the Camargos Reservoir.	-21.613229°, -44.397045°
Trans1	Transition	The transition region of the Grande River, between its lotic stretch with the Camargos Reservoir.	-21.462530°, -44.391532°
Trans2	Transition	The transition region of the Aiuruoca River between its lotic stretch with the Camargos Reservoir.	-21.479907°, -44.456347°
Trans3	Transition	The Camargos Reservoir at the confluence of the Aiuruoca and Grande rivers.	-21.444272°, -44.448429°
Cam1	Camargos	The Camargos Reservoir about 11 km downstream from the previous point.	-21.397605°, -44.520289°
Cam2	Camargos	The Camargos Reservoir about 11 km downstream from the previous point.	-21.337780°, -44.539758°
Cam3	Camargos	The Camargos Reservoir about 11 km downstream from the previous point.	-21.344771°, -4.609349°
Itu1	Itutinga	Downstream of Camargos Dam near its escape channel and upstream of Itutinga Dam.	-21.322170°, -44.614583°
Itu2	Itutinga	The Itutinga Reservoir near its dam.	-21.294487°, -44.617696°
MLA1	Aiuruoca marginal lagoon	About 600 m from Riv2. Absence of native riparian forest with high anthropic influence. Perennial lagoon.	-21.7107°, -44.4095°
MLA2	Aiuruoca marginal lagoon	About 400 m from Riv2. Deep and perennial lagoon, close to sand extraction.	-21.7036°, -44.4061°
MLA3	Aiuruoca marginal lagoon	About 4 km from Riv4. Deep, large and perennial lagoon with native riparian forest and human influence.	-21.6455°, -44.388°
MLA4	Aiuruoca marginal lagoon	About 2 km from Riv2. Native riparian forest nearby and human influence. Shallow and intermittent lagoon.	-21.7133°, -44.3933°
MLG1	Grande marginal lagoon	About 6 km from Riv1. Native riparian forest nearby, presence of macrophytes and vegetation on the shores. Can get a lot wider in wet season.	-21.5192°, -44.1602°
MLG2	Grande marginal lagoon	About 6 km from Riv1. Native riparian forest nearby and human influence. Used by cattle. During high flood, it can connect with other smaller lagoons and get a lot wider.	-21.5228°, -44.1674°
MLG3	Grande marginal lagoon	About 2.5 km from Riv1. Presence of native riparian forest and human influence. Used by cattle. During high flood, it can get large and deep.	-21.486786°, -44.1870°
MLG4	Grande marginal lagoon	About 6 km from Riv1. Large lagoon with native riparian forest. During high flood, it can get large and deep. Little human influence.	-21.4872°, -44.1786°

Table 3. Numeric abundance of migratory fish species collected from the Upper Grande River and CI-UFLA voucher number. Legend: Samples realized between 03/2019 to 12/2021. The values within parentheses and brackets in marginal lagoons represent juveniles and in sites represent fingerlings, respectively. R1 = Riv1; R2 = Riv2; R3 = Riv3; R4 = Riv4; T1 = Trans1; T2 = Trans2; T3 = Trans3; C1 = Cam1; C2 = Cam2; C3 = Cam3; I1 = Itu1; I2 = Itu2; LA1 = MLA1; LA2 = MLA2; LA3 = MLA3; LA4 = MLA4; LG1 = MLG1; LG2 = MLG2; LG3 = MLG3; LG4 = MLG4.

Taxon	R1	R2	R3	R4	T1	T2	T3	C1	C2	C3	I1	I2	LA1	LA2	LA3	LA4	LG1	LG2	LG3	LG4	Voucher
Characiformes																					
Anostomidae																					
Leporinus friderici	15	10	37	14	10	8	18	11[2]	9	3	1	1	0	0	0	0	0	0	0	0	1263
Megaleporinus obtusidens	1	3	0	2	0	1	0	0	5	0	0	0	0	0	0	0	0	0	0	0	1264
Megaleporinus piavussu	2	4	4	5	12	11	3	3	1	2	3	0	0	0	0	0	1 (0)	0	0	0	1271
Bryconidae																					
Brycon orbignyanus	0	0	1	0	1	0	0	0	1	3	13	1	0	0	0	0	0	0	0	0	1261
Salminus hilarii	14	6	10	31	4	7	1	1	0	1	0	0	5(5)	0	10(10)	6(6)	8(8)	1(1)	0	0	1273
Prochilodontidae																					
Prochilodus lineatus	2	2	0	0	0	0	0	1	0	2	11	0	3(2)	0	0	0	0	1(1)	0	0	1289
Siluriformes																					
Pimelodidae																					
Pimelodus maculatus	6	23	33	29	42	47	61	25	38	79	52	18	10(1)	0	17(1)	0	1 (0)	25(1)	0	45(2)	1268
Total abundance	40	48	85	81	69	74	83	41	54	90	80	20	18	0	27	6	10	27	0	45	
Total richness	6	6	5	5	5	5	4	5	5	6	5	3	3	0	2	1	3	3	0	1	

were sampled. They were found in the lotic stretches, while *Pimelodus maculatus* Lacepède, 1803 was registered throughout the entire sampled area (Fig. 3).

The stages of gonadal maturation varied from one species to another, and among regions and seasons. In general, the final stages (mature and post-spawning) were prevalent during the wet season and more frequent in free-flowing rivers and transition zones (Fig. 4). There were juveniles of *P. maculatus* in almost every sampling location, but individuals in initial maturation and post-spawning stages were also prevalent, being captured in free-flowing rivers and transition areas during the wet season. There were individuals of *Brycon orbignyanus* (Valenciennes, 1850) and *Prochilodus lineatus* (Valenciennes, 1837) in the post-spawning stage in the Itutinga Reservoir, but with signs of follicular atresia. The numbers of individuals of *L. friderici* and other species in the post-spawning stage increased in free-flowing rivers during the wet season. The majority of *Megaleporinus piavussu* (Britski, Birindelli & Garavello, 2012) adults and juveniles was found in transition areas, with more individuals in the post-spawning stage. Adults of *Megaleporinus obtusidens* (Valenciennes, 1837) were not found in free-flowing rivers and transition areas, despite the juveniles sampled in these areas during the wet season. Adults in mature and post-spawning stages and juveniles of *Salminus hilarii* Valenciennes, 1850 were only found in free-flowing rivers and transition areas and mainly during the wet season.

DISCUSSION

The numbers, biomass, and richness of migratory fishes differed among regions, and slightly decreased along the gradient surveyed. Migratory fishes were found in greater numbers of individuals and species in rivers and in the transition zone. The biomass decreased from the uppermost to the downmost region, except for Itutinga, possibly due to fish stocking. Juveniles and fingerlings were captured in low numbers of individuals and species richness was also low, indicating that recruitment does not occur in the river-reservoir transition areas. On the other hand, marginal lagoons seem to present an important environment for the early development of migratory fishes, since four of the seven species were captured in these areas. Mature individuals, which were more frequent in rivers and transition sites, were found during the wet season. The system is used differently by the different migratory species. Most species were found in low numbers in lentic sites and seemed to depend on stretches of free-flowing rivers to complete their life cycles.

The species richness of migratory fishes recorded in our study represents 78% of the total number of native migratory species from the Upper Grande River (Santos 2010). Only *Zungaru jahu* (Ihering, 1898) and *Salminus brasiliensis* (Cuvier, 1816) were not sampled. These species have large body sizes and specific adaptations for migration and reproduction (Agostinho et al. 2003, Zaniboni-Filho et al. 2017)

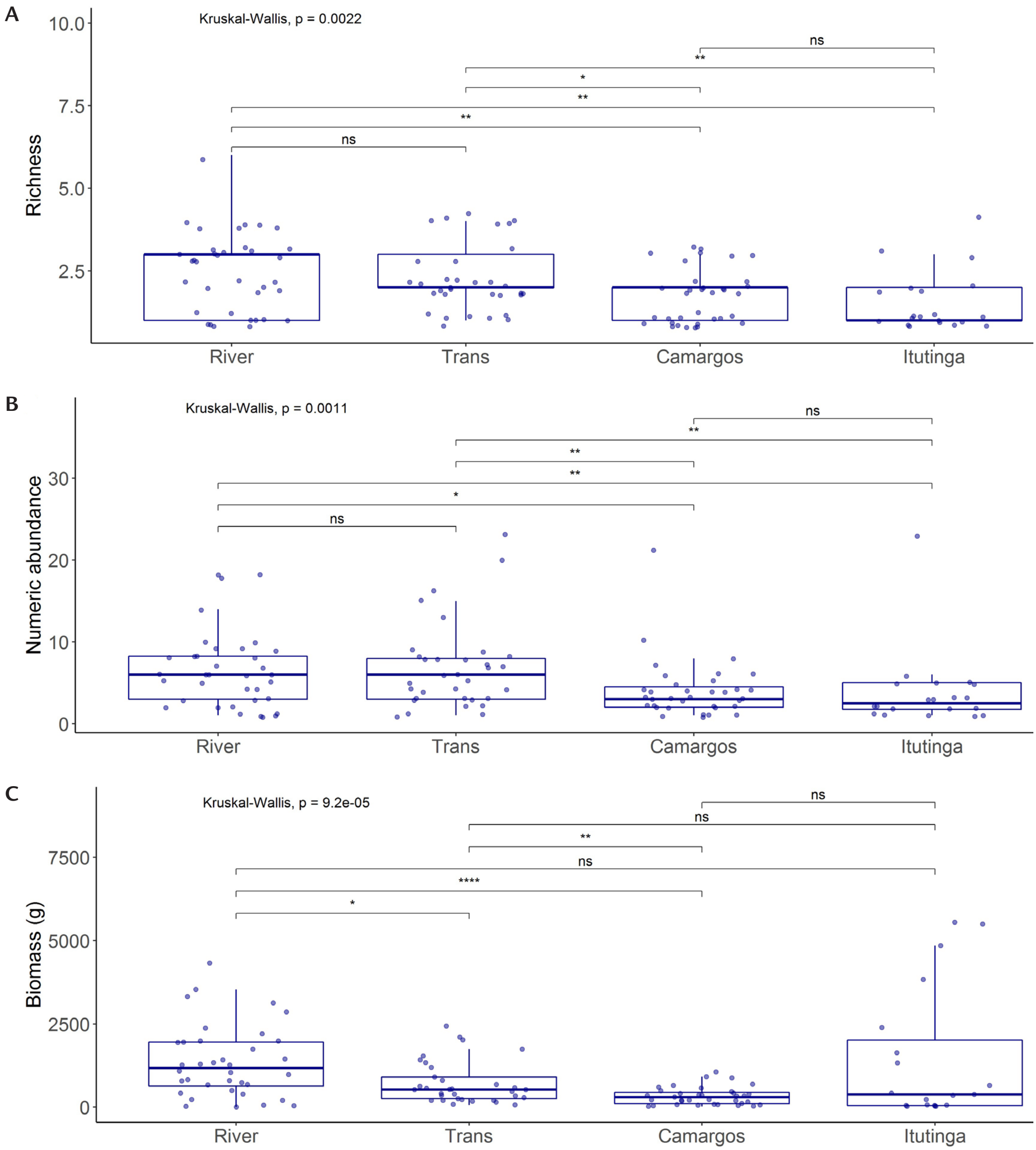

Figure 2. Variation (median ± interquartile range and amplitude) along the groups: (A) fish richness; (B) fish numeric abundance; (C) fish abundance.

but are highly impacted by dams (De Fries et al. 2019). The loss of a connection, due to a sequence of impoundments, can impede large migratory fishes from accessing the upper parts of the basin (Petesse and Petrere 2012 Pelicice et al. 2015, Lopes et al. 2018).

We observed a greater biomass in river and transition zones, most likely because these migratory species prefer flowing waters to lentic areas (Pompeu et al. 2012, Agostinho et al. 2016). In addition, reservoir cascade systems tend to reduce local connectivity, leading to a loss of habitats for

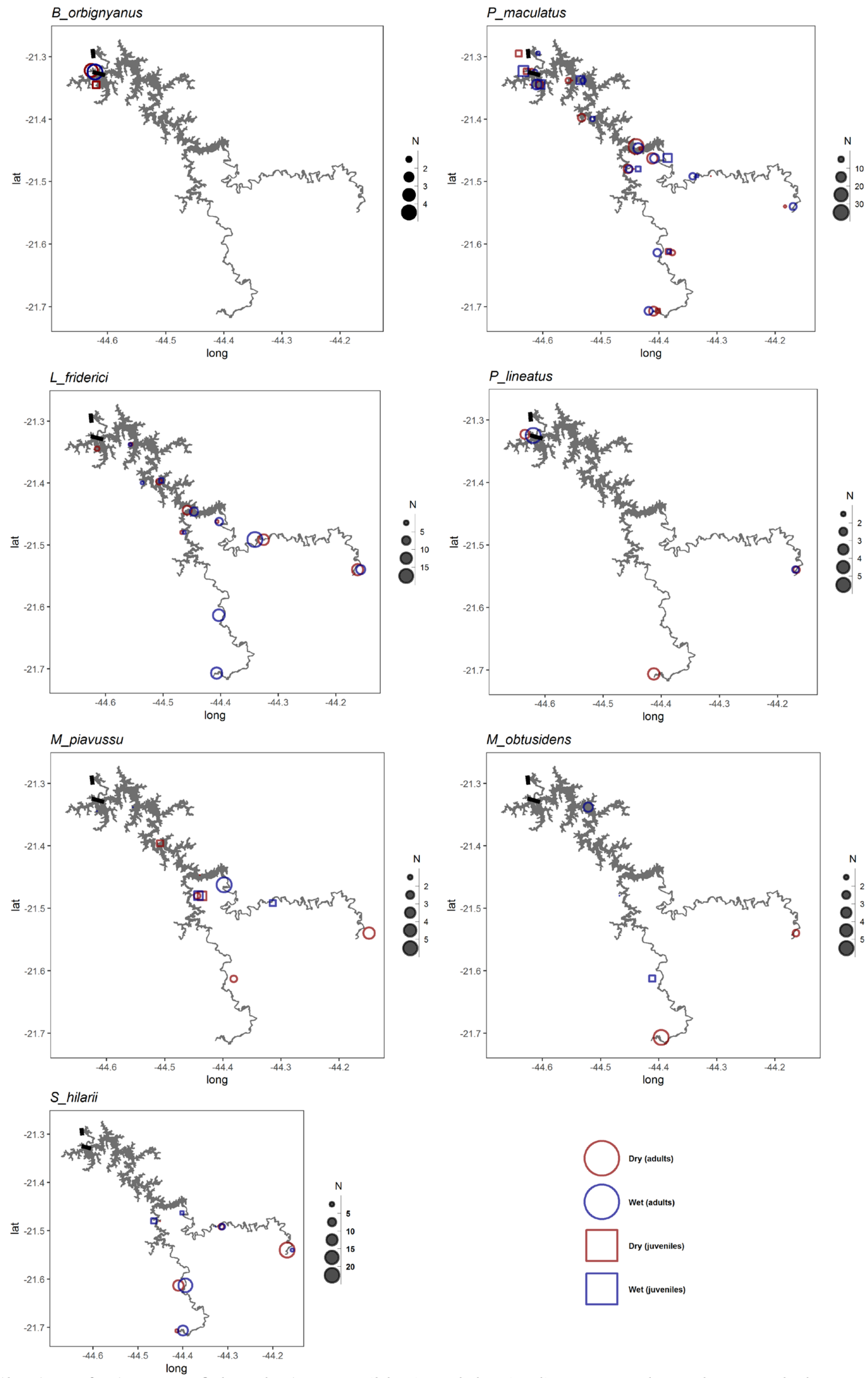

Figure 3. Distribution of migratory fishes during wet (blue) and dry (red) seasons along the sampled system. Represented by adults (ball) and juveniles (square) in both seasons. The symbol size indicates fish abundance.

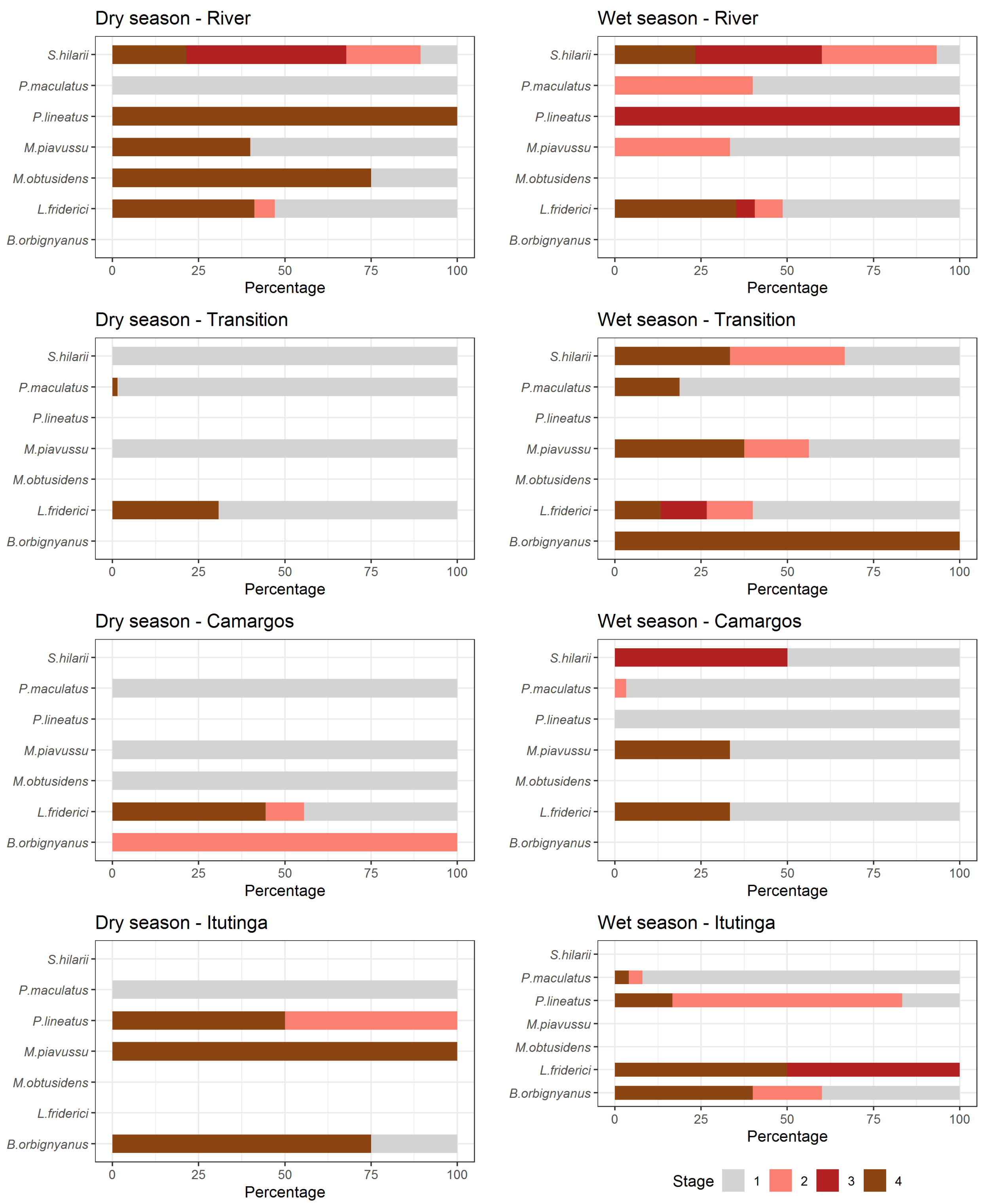

Figure 4. Gonadal maturation stage of migratory species during the wet (right side) and dry (left side) seasons in each group. Groups formed in the system by gonadal maturation stage: 1) immature, 2) initial maturation, 3) mature; 4) post-spawning.

migratory species and, consequently, a loss of richness and abundance (Cheng et al. 2015, Loures and Pompeu 2018). Such pattern was not evident in our study, possibly because this system is composed of only two medium-sized reservoirs, and migratory fish stocking (mainly *B. orbignyanus* and *P. lineatus*) happened in the Itutinga (Alves et al. 1998) and Camargos reservoirs. Therefore, since there is not a self-sustainable population of migratory fishes in the lowermost reservoir (Itutinga), our data suggest that fish stocking may eventually mask important ecological gradients.

The eventual displacements of migratory species could result in seasonal differences in the structure of their assemblages along the studied gradient, especially in regions connected to the lotic remnant. However, none of the regions showed seasonal differences in richness, numeric abundance and biomass. For the transition region and Camargos, such a pattern indicates that these areas do not play a relevant role in the life cycle of these species, although they are continuously occupied by them. The absence of seasonal differences in the sampled riverine stretches suggests that breeding sites must be located further up the sampled sites. In the case of self-sustainable populations, the spawning site is located far enough to enable the development of ichthyoplankton, preventing larvae from drifting to inappropriate places, such as reservoirs (Olden 2016). Furthermore, the great abundance of *P. maculatus*, whose migratory nature is controversial, may have masked possible patterns.

Fingerling and juvenile stages were not abundant within the river-reservoir transition sites, indicating that they did not contribute to migratory fish recruitment. The extreme water level fluctuations due to the operational requirements of the Camargos Dam decreases the habitats and refuge areas available for them (Nobile et al. 2019). Therefore, the migratory species found in the studied systems rely on the abundant floodplain lagoons along the Aiuruoca (Lima et al. 2010) and the Grande rivers to complete their life cycle. In addition, Suzuki et al. (2011) sampled considerable amounts of eggs at the free-flowing stretches upstream of the Camargos Dam, at the Grande and Aiuruoca rivers, indicating that the upper stretches of both rivers are used for spawning and floodplains for their early development. Presumably, after that, when the water level drops, the juveniles recruited at the floodplains return to the river in search of their feeding areas (Agostinho et al. 2003, Silva et al. 2015).

Juveniles and adults of *Pimelodus maculatus* were found in almost all groups and seasons, although individuals in mature and post-spawning gonadal maturation stages had been found mainly in free-flowing rivers and river-reservoir transition areas during the wet season. There are questions as to whether *P. maculatus* can be considered a migratory species. (Santos et al. 2012, Zaniboni-Filho and Schulz 2003 Oldani et al. 2007, Arcifa and Esguícero 2012). According to Agostinho et al. (2003), it probably needs fewer free stretches of river to complete its life cycle. In the Paraná River Basin, *P. maculatus* is considered widely distributed (Agostinho et al. 2003), even in reservoirs (Agostinho et al. 2007a), as demonstrated by its dominance in five cascade reservoirs in the Araguari River (Loures and Pompeu 2018). Although juveniles have been previously collected from the Itutinga Reservoir, which has no free-flowing stretches or important tributaries, most of the adults presented the immature gonadal stage and no fingerlings were captured, indicating that they were found there because individuals are passing through the spillway or turbines of the Camargos Dam (Alves et al. 1998).

Samples of *Brycon orbignyanus* and *P. lineatus* in the post-spawning stage were found within the Itutinga Reservoir, although no juvenile or fingerlings were collected in this area. Juveniles of *B. orbignyanus* were sampled in the Camargos Reservoir. The first is categorized as an endangered species (Akama et al. 2018). The decline in the numbers of *B. orbignyanus* has been linked to the changes in the original flood regimen, especially changes caused by dam constructions, and removal of riparian vegetation (Tonella et al. 2019). *P. lineatus* travels hundreds of kilometers to reproduce (Makrakis et al. 2012) and the decline in the number of individuals of this species is also associated with an interruption in the connectivity between habitats caused by dams, and also overfishing (Baigun et al. 2013). Both species depend on specific environmental conditions such as free-flowing rivers and nursery areas to complete their life cycles (Agostinho et al. 2003, Zaniboni-Filho and Schulz 2003). Their presence in the study area is probably associated with fish stocking, implemented by the local power company (CEMIG) at Itutinga (Alves et al. 1998) and Camargos reservoirs until 2019.

As expected for a species depending on free-flowing rivers for reproduction (Resende 2003, Agostinho 2007a), the frequency of capture of *L. friderici* increased in the free-flowing rivers during the wet season. An increase in the number of individuals in the post-spawning stage in these areas was observed at the same period. *L. friderici* individuals, which inhabit reservoirs, depend on lotic environments to reproduce (Lopes et al. 2000). This species was the only one for which we collected fingerlings and juveniles, suggesting that its recruitment might occur at the river-reservoir transition areas. However, it is important to confirm whether these areas are often used for recruitment or weather the occurrence of *L. friderici* there is sporadic.

In the cascade reservoir system with important free-flowing river stretches, upstream of the Camargos reservoir, we verified that migratory fish reproduction seems to depend on the free-flowing rivers and their associated floodplains. On the other hand, river-reservoir transition areas do not seem to play a significant role in recruitment. Therefore, the lotic stretches of the Grande and Aiuruoca rivers seem to maintain self-sustainable populations of the registered migratory species, acting as source areas for the individuals that use the reservoirs. In this sense, we highlight the importance of maintaining these free-flowing rivers and the conservation of their floodplains. Finally, we encourage further research aiming to investigate migratory fishes and icthyoplankton in the upper stretches of the Grande and Aiuruoca rivers, including their headwaters, to confirm the observed patterns. The maintenance of free-flowing stretches upstream of reservoirs and tributaries should be considered when planning new hydropower plants. This could help attenuate the regional impacts of these plants, especially on migratory fishes.

ACKNOWLEDGEMENTS

We thank Companhia Energética de Minas Gerais (CEMIG) and the Aneel Research & Development Program (Programa de P&D) for funding the P&D project GT612. We also thank the Fish Ecology Laboratory for supporting the development of this study in the field and in the laboratory. We thank André Maciel da Silva Sene for the support review. Finally, we thank the Universidade Federal de Lavras (UFLA) for the support and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, CAPES) for the master's scholarship. PSP received a research fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq, 303548/2017-7).

LITERATURE CITED

Agostinho AA, Gomes LC, Suzuki HI, Júlio HF Jr (2003) Migratory Fishes of the Upper Paraná River Basin. In: Carosfeld J, Harvey B, Ross C, Baer A (Eds) Migratory Fishes of South America: biology, fisheries and conservation status. World Bank, Washington, DC, 19–98.

Agostinho AA, Gomes LC, Pelicice FMA (2007a) Ictiofauna Sul-Americana: composição e história de vida. In: Agostinho AA, Gomes LC, Pelicice FM (Eds) Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil. EDUEM, Maringá, 10–37.

Agostinho AA, Gomes LC, Santos NCL, Ortega JCG, Pelicice FM (2016) Fish assemblages in Neotropical reservoirs: Colonization patterns, impacts and management. Fisheries Research 173: 26–36. https://doi.org/10.1016/j.fishres.2015.04.006

Agostinho AA, Marques EE, Agostinho CS, Almeida DA, Oliveira RJ, Melo JRB (2007b) Fish ladder of Lajeado Dam: Migrations on one-way routes? Neotropical Ichthyology 5(2): 121–130. https://doi.org/10.1590/S1679-62252007000200005

Akama A, Netto-Ferreira AL, Zanata AM, Calegari BB, Figueiredo CAA, Alves CBM, Cramer CA, Zawadzki CH, et al. (2018) *Brycon orbignyanus* In: Instituto Chico Mendes de Conservação da Biodiversidade (Org) Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. ICMBio, Brasília, vol. 1, 91–94.

Alves CBM, Godinho AL, Godinho HP, Torquato VC (1998) A ictiofauna da represa de Itutinga, Rio Grande (Minas Gerais, Brasil). Revista Brasileira de Biologia 58(1): 121–129.

Arcifa MS, Esguícero ALH (2012) The fish fauna in the fish passage at the Ourinhos Dam, Paranapanema River. Neotropical Ichthyology 10(4): 715–722. https://doi.org/10.1590/S1679-62252012000400004

Baigún C, Minotti P, Oldani N (2013) Assessment of sábalo (*Prochilodus lineatus*) fisheries in the lower Paraná River Basin (Argentina) based on hydrological, biological, and fishery indicators. Neotropical Ichthyology 11: 199–210. https://doi.org/10.1590/S1679-62252013000100023

Borges GC, Abjaudi GA (2016) Caracterização ambiental da bacia do Rio Grande. In: Melo RMC, Borges GC (Eds) Rio Grande: Ambiente, Peixes e Pessoas. Instituto de Estudos Pro-Cidadania, Belo Horizonte, 8–101.

Cachapuz PBB (2006) Usinas da Cemig: a história da eletricidade em Minas e no Brasil, 1952–2005. Centro de Memória da Eletricidade no Brasil, Rio de Janeiro, 304 pp.

Carvajal-Quintero J, Villalobos F, Oberdorff T, Grenouillet G, Brosse S, Hugueny B, Jézéquel C, Tedesco PA (2019) Drainage network position and historical connectivity explain global patterns in freshwater fishes range size. PNAS 116(27): 13434–13439. https://doi.org/10.1073/pnas.1902484116

Cheng F, Li W, Castello L, Murphy BR, Xie S (2015) Potential effects of dam cascade on fish: lessons from the Yangtze River. Reviews in Fish Biology and Fisheries 25: 569–585. https://doi.org/10.1007/s11160-015-9395-9

De Fries L, Hahn L, Meneses BA, Câmara LF, Becker FG, Hartz SM (2019) Movement and longitudinal distribution of a migratory fish (*Salminus brasiliensis*) in a small reservoir in southern Brazil. Neotropical Ichthyology 17(3): e180119. https://doi.org/10.1590/1982-0224-20180119

Esguícero ALH, Arcifa MS (2010) Fragmentation of a Neotropical migratory fish population by a century-old dam. Hydrobiologia 638: 41–53. https://doi.org/10.1007/s10750-009-0008-2

Gomes LC, Miranda LE (2001) Riverine characteristics dictate composition of fish assemblages and limit fisheries in reservoirs of the Upper Paraná River basin. Regulated Rivers: Research & Management 17(1): 67–76. https://doi.org/10.1002/1099-1646(200101/02)17:1<67::AID-RRR615>3.0.CO;2-P

Harvey B, Carosfeld J (2003) Introduction: Fishes of the Floods. In: Carosfeld J, Harvey B, Ross C, Baer A (Eds) Migratory Fishes of South America: Biology, Fisheries and Conservation status. World Bank, Washington DC, 1–18.

Lima LPZ, Pompeu PS, Suzuki FM, Carvalho LMT (2010) Dinâmica espacial de lagoas marginais presentes no rio Aiuruoca, MG, em períodos de cheia e seca. Revista Brasileira de Biociências 8(3): 253–256.

Lopes JM, Alves CBM, Peressin A, Pompeu PS (2018) Influence of rainfall, hydrological fluctuations, and lunar phase on spawning migration timing of the Neotropical fish *Prochilodus costatus*. Hydrobiologia 818: 145–161. https://doi.org/10.1007/s10750-018-3601-4

Lopes CA, Benedito-Cecilio E, Agostinho AA (2000) The Reproductive Strategy of *Leporinus friderici* (Characiformes, Anostomidae) in the Paraná River Basin: The Effect of Reservoirs. Revista Brasileira de Biologia 60(2): 255–266. https://doi.org/10.1590/S0034-71082000000200009

Lopes JM, Pompeu PS, Alves CBM, Peressin A, Prado IG, Suzuki FM, Facchin S, Kalapothakis E (2019) The critical importance of an undammed river segment to the reproductive cycle of a migratory Neotropical fish. Ecology of Freshwater Fish 28: 302–316. https://doi.org/10.1111/eff.12454

Loures RC, Pompeu PS (2018) Long-term study of reservoir cascade in Southeastern Brazil reveals spatio-temporal gradient in fish assemblages. Marine and Freshwater Research 69(12): 1983–1994. https://doi.org/10.1071/MF18109

Lucas MC, Baras E (2001) Migration of freshwater fishes. Blackwell Science, Osney Mead, 420 pp.

Makrakis MC, Miranda LE, Makrakis S, Fontes HM, Morlis WG, Dias JHP, Garcia JO (2012) Diversity in migratory patterns among Neotropical fishes. Journal of Fish Biology 81: 866–881. https://doi.org/10.1111/j.1095-8649.2012.03346.x

Marques H, Dias JHP, Perbiche-Neves G, Kashiwaqui EAL, Ramos IP (2018) Importance of dam-free tributaries for conserving fish biodiversity in Neotropical reservoirs. Biological Conservation 224: 347–354. https://doi.org/10.1016/j.biocon.2018.05.027

Nakatani K, Agostinho AA, Baumgartner G, Bialetzki A, Sanches PV, Makrakis MC, Pavanelli CS (2001) Ovos e larvas de peixes de água doce: Desenvolvimento e manual de identificação. EDUEM, Maringá, 378 pp.

Nobile AB, Freitas-Souza D, Lima FP, Queiroz J, Bayona-Perez IL, Carvalho ED, Ramos IP (2019) Damming and seasonality as modulators of fish community structure in a small tributary. Ecology of Freshwater Fish 28: 563–572. https://doi.org/10.1111/eff.12475

Oksanen JF, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin DM, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020) Vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Oldani NO, Baigún CRM, Nestler JM, Goodwin RA (2007) Is fish passage technology saving fish resources in the lower La Plata River basin? Neotropical Ichthyology 5(2): 89–102. https://doi.org/10.1590/S1679-62252007000200002

Olden JD (2016) Challenges and opportunities for fish conservation in dam-impacted water. In: Closs GP, Krkosek M, Olden JD (Eds) Conservation of freshwater fishes. Cambridge University Press, Cambridge, 107–148.

Ota RR, Deprá GC, Graça WJ, Pavanelli CS (2018) Peixes da planície de inundação do alto rio Paraná e áreas adjacentes: revised, annotated and updated. Neotropical Ichthyology 16(2): 1–111. https://doi.org/10.1590/1982-0224-20170094

Pelicice FM, Agostinho AA (2008) Fish-passage facilities as ecological traps in large neotropical rivers. Conservation Biology 22(1): 180–188. https://doi.org/10.1111/j.1523-1739.2007.00849.x

Pelicice FM, Azevedo-Santos VM, Esguícero ALH, Agostinho AA, Arcifa MS (2018) Fish diversity in the cascade of reservoirs along the Paranapanema River, southeast Brazil. Neotropical Ichthyology 16(2): 1–18. https://doi.org/10.1590/1982-0224-20170150

Pelicice FM, Pompeu PS, Agostinho AA (2015) Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. Fish and Fisheries 16(4): 697–715. https://doi.org/10.1111/faf.12089

Petesse ML, Petrere M Jr (2012) Tendency towards homogenization in fish assemblages in the cascade reservoir system of the Tietê river basin, Brazil. Ecological Engineering 48: 109–116. https://doi.org/10.1016/j.ecoleng.2011.06.033

Pompeu PS, Agostinho AA, Pelicice FM (2012) Existing and future challenges: the concept of successful fish passage in South America. River Research and Applications 28: 504–512. https://doi.org/10.1002/rra.1557

Resende EK (2003) Migratory Fishes of the Paraguay-Paraná Basin, Excluding the Upper Paraná Basin. In: Carosfeld J, Harvey B, Ross C, Baer A (Eds) Migratory Fishes of South America: Biology, Fisheries and Conservation status. World Bank, Washington, DC, 99–156.

Ribeiro DC, Chagas JMA, Thereza MR, Langeani F (2019) Checklist and key for the identification of fish fauna of the Uberaba River, Upper Paraná River system, Brazil. ZooKeys 875: 129–155. https://doi.org/10.3897/zookeys.875.31977

RStudio Team (2021) RStudio: Integrated Development Environment for R. RStudio, PBC, Boston. http://www.rstudio.com

Santos ABI, Albieri RJ, Araújo FG (2012) Influences of dams with different levels of river connectivity on the fish community structure along a tropical river in Southeastern Brazil. Journal of Applied Ichthyology 29(1): 1–9. https://doi.org/10.1111/jai.12027

Santos GB (2010) A Ictiofauna da bacia do Alto Paraná (rio Grande e rio Paranaíba). MG BIOTA 2: 5–25.

Santos NCL, García-Berthou E, Dias JD, Lopes TM, Affonso IP, Severi W, Gomes LC, Agostinho AA (2018) Cumulative ecological effects of a Neotropical reservoir cascade across multiple assemblages. Hydrobiologia 819(1): 77–91. https://doi.org/10.1007/s10750-018-3630-z

Santos NCL, Santana HS, Ortega JCG, Dias RM, Stegmann LF, Araújo IMS, Severi W, Bini LM, Gomes LC, Agostinho AA (2017) Environmental filters predict the trait composition of fish communities in reservoir cascades. Hydrobiologia 802(1): 245–253. https://doi.org/10.1007/s10750-017-3274-4

Silva FO, Andrade FR Neto, Silva SH, Silva JO, Zamboni Filho E, Prado IG, Peressin A, Pelicice FM (2020) Recruitment dynamics of a migratory fish in a semiarid river system. Inland Waters 10: 529–541. https://doi.org/10.1080/20442041.2020.1805977

Silva PS, Makrakis MC, Miranda LE, Makrakis S, Assumpção L, Paula S, Dias JHP, Marques H (2015) Importance of reservoir tributaries to spawning of migratory fish in the Upper Paraná River. River Research and Applications 31: 313– 322. https://doi.org/10.1002/rra.2755

Souza RCR (2013) Distribuição e Composição do Ictioplâncton no Reservatório de Três Marias, MG, Brasil. MSc Thesis, Universidade Federal de Lavras, Lavras, Minas Gerais, Brazil. http://repositorio.ufla.br/jspui/handle/1/764

Suzuki FM, Pires LV, Pompeu PS (2011) Passage of fish larvae and eggs through the Funil, Itutinga and Camargos reservoirs on the upper Rio Grande (Minas Gerais, Brazil). Neotropical Ichthyology 9(3): 617–622. https://doi.org/10.1590/S1679-62252011000300014

Tonella LH, Dias RM, Vitorino Junior OB, Fugi R, Agostinho AA (2019) Conservation status and bio-ecology of *Brycon orbignyanus* (Characiformes: Bryconidae), an endemic fish species from the Paraná River basin (Brazil) threatened with extinction. Neotropical Ichthyology 17(3): e190030. https://doi.org/10.1590/1982-0224-20190030

Vazzoler AEAM (1996) Biologia da reprodução de peixes teleósteos: teoria e prática. EDUEM, Maringá, 169 pp.

Winemiller KO, McIntyre PB, Castello L, Fluet-Chouinard E, Giarrizzo T, Nam S, Baird IG, Darwall W, et al. (2016) Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science 351(6269): 128–129. https://doi.org/10.1126/science.aac7082

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, 260 pp.

Zaniboni-Filho E, Ribolli J, Hermes-Silva S, Nuñer AP (2017) Wide reproductive period of a long-distance migratory fish in a subtropical river, Brazil. Neotropical Ichthyology 15(1): e160135. https://doi.org/10.1590/1982-0224-20160135

Zaniboni-Filho E, Schulz UH (2003) Migratory Fishes of the Uruguay River. In: Carosfeld J, Harvey B, Ross C, Baer A (Eds) Migratory Fishes of South America: Biology, Fisheries and Conservation status. World Bank, Washington, DC, 157–194.

Submitted: August 19, 2022
Accepted: March 8, 2023
Editorial responsibility: Vinicius Abilhoa

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Competing Interests

The authors have declared that no competing interests exist.

How to cite this article

Silva-Sene AM, Fontes RCL, Prado IG, Pompeu PS (2023) Migratory fishes from rivers to reservoirs: seasonal and longitudinal perspectives. Zoologia 40: e22044. https://doi.org/10.1590/S1984-4689.v40.e22044

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